# ORIGIN OF THE PALAEOKARST IN MIOCENE EVAPORITES ON THE SW PERIPHERY OF THE EASTERN EUROPEAN PLATFORM IN THE LIGHT OF PALYNOLOGICAL STUDIES – A CASE STUDY OF THE ZOLOUSHKA CAVE, BUKOVINA, WESTERN UKRAINE

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**Abstract:** The Zoloushka Cave belongs to a group of the largest gypsum caves in Western Ukraine (Bukovina region), developed in the middle Miocene (upper Badenian) evaporite series (Tyras Formation) on the SW periphery of the East European Platform. It is developed in the lower part of the evaporite series composed of gypsum, which is covered by a carbonate layer (Ratyn Limestone). The uneven upper surface of the gypsum at the contact with the limestone, the frequent occurrence of palaeokarst forms, and the presence of karstified fissures filled with allochthonous material indicate a sedimentation break between the gypsum and the overlying limestone. To support this thesis and to add new data on the age and palaeoenvironmental conditions of palaeokarst formation in the Bukovina region, palynological studies were carried out on material from the Zoloushka Cave. Palynofacies, sporomorphs and dinoflagellate cysts were studied. In total, over 70 sporomorph taxa and over 25 dinoflagellate cyst taxa have been identified in four samples collected from the filling of the palaeokarstic forms in the cave. The results of the analysis of sporomorphs and dinoflagellate cysts point to the formation of the palaeokarst during the sedimentation break that took place at the end of the late Badenian evaporitic cycle in the Western Ukraine region. The subsequent marine transgression led to the filling of the karst forms in gypsum with chemogenic carbonate material, precipitated from marine water (draperies) and with fine-grained, clastic material (pockets and fissures).

Key words: palaeokarst, palynology, sporomorphs, dinoflagellate cysts, caves, Western Ukraine, Eastern European Platform, Badenian.

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### **INTRODUCTION**

Evaporite rocks, such as gypsum, anhydrite and halite, owing to their high solubility in water, are among those rocks that most easily undergo karstification. Karst forms, originating both at the rock surface (karren, dolines of dissolution, karstified fissures, etc.) and within rock bodies (caverns and caves) are frequently filled with various deposits that commonly contain organic components. The latter, in the case of fossil karst forms, i.e., palaeokarst, may serve as a source of information about the age of its formation and the palaeoenvironmental conditions associated with the karstification processes (e.g., Bosák *et al.*, 1989; Carrión *et al.*, 1999). Palynomorphs, both terrestrial (e.g., pollen grains and spores) and aquatic (e.g., green algae or dinoflagellate cysts) are among those fossils that because of their high mobility (i.e., pollen grains, especially their saccate forms, easily transported by both wind and water) can penetrate into karstified fissures and karst cavities. Despite this, studies dealing with palynological matter from the Neogene karst deposits are rather rare in world literature (e.g.,Takahashi and Jux, 1982; Walsh *et al.*, 1996; Hansen *et al.*, 2001; Shunk *et al.*, 2009; Worobiec and Szulc, 2010; Worobiec, 2011; Ochoa *et al.*, 2012; Szulc and Worobiec, 2012; Worobiec *et al.*, 2013) and most of them deal with palaeosinkhole deposits.



Fig. 1. Distribution of sulphate rocks of the Miocene evaporitic formation in the northern (Polish) and north-eastern (Ukrainian) parts of the Carpathian Mountains with location of the Zoloushka Cave.

In the present study, the authors applied classical spore-pollen analysis (E.W.) together with the study of dino-flagellate cysts (P.G.) and other non-pollen palynomorphs, as well as palynofacies analysis (G.W.) of palaeokarst formations and cave deposits in the Zoloushka (Cinderella) Cave at Bukovina (Western Ukraine). The Zoloushka Cave is one of many caves developed in the upper Badenian evaporite series of the SW part of the East European Platform, adjacent to the Carpathian Foredeep (Fig. 1).

The origin of karstification of the upper part of the gypsum series (at the contact with limestone) and the relation of the host deposits (gypsum) to the overlying strata (limestone) have not yet been fully elucidated. According to Andreychouk (2007), the uneven contact between these two units (Fig. 2) can reflect either erosional (karstification of a gypsum surface during a short sedimentation break that preceded the accumulation of the Ratyn Limestone), or metasomatic (transformation of gypsum into limestone). It should be noted that on the scale of the whole area of the Western Ukraine Gypsum Karst Region, the question of the sedimentation break and karstification of the gypsum just after the end of deposition is barely recognized. The sparse literature on this subject does not deal directly with the question (e.g., Lomayev, 1979). Klimchouk (2007), on the basis of the studies of sulphur deposits from this region, genetically associated with evaporites, came to the conclusion



Fig. 2. Uneven contact between the gypsum (lower part) and the Ratyn Limestone (upper part). Pictures A and B represent some examples from different places in the Zoloushka Cave.



Fig. 3. Geological cross-section of the Zoloushka Cave area (Andreychouk, 2007).

that the uneven contact between the gypsum and the limestone can be of a metasomatic nature. The results of the palynological studies of the samples from the Zoloushka Cave presented in the present paper provide new data concerning the origin, age and palaeoenvironmental conditions of palaeokarst formation in the Bukovina region.

# **GEOLOGICAL BACKGROUND**

The evaporites of the study area belong to the upper Badenian Tyras Formation (Andreyeva-Grigorovich *et al.*, 1997). They rest on the lower Badenian greenish gray marls of the Baranov Beds ( $N_1bd_1 - 0-4$  m thick), which cover an uneven, eroded substrate surface composed of carbonate-sandy Cenomanian deposits: fractured limestone ( $K_2s_2$ , 3–5 m thick) in the upper part, and quartz-glauconitic sandstone ( $K_2s_1$ ; 10–13 m thick) in the lower part of the profile (Fig. 3).

The evaporites consist of two lithological facies: a lower one developed as sulphates and an upper facies developed as carbonates (Ratyn Limestone); together they are also known as the so-called Dnister Beds. The cave is developed in lower gypsum facies.

The lower (gypsum) facies is represented by coarsely crystalline gypsum (20–25 m thick) and the upper one, by chemogenic limestone (0.7–1.2 m thick). The gypsum rocks are characterized by a high chemical purity (the content of  $CaSO_4 \cdot 2H_2O$  reaches there up to 97%; Andreychouk, 2007) that makes them very susceptible to dissolution. The entire gypsum series consists of four major units that differ in structure and texture. The uppermost unit (interval 0–7 m) is made up of large- and medium-sized gypsum crystals. Below (7–15 m) them, a laminated unit occurs; it consists of interlayered medium- and small-sized gypsum crystal beds. It is underlain by finely crystalline, laminated gypsum (15–19 m), and by a cryptocrystalline (aphanic) gypsum unit (19–25 m). The boundaries between these four units have a transitional character (Andreychouk, 2007).

The Ratyn Limestone, which covers the gypsum, is a pelitomorphic, chemogenic limestone that shows a compact, crystalline texture; it is commonly cracked and it has a platy structure (Andreychouk, 2007). The contact between

these two units (i.e. gypsum and limestone) is usually uneven (Fig. 2), commonly emphasized also by corrosive structures. Occasionally, a thin (1-3 cm) layer of clayey gypsum occurs between the gypsum and the limestone.

The top of the evaporite series, i.e., the top of the Ratyn Limestone, is covered by laminated bluish gray loamy-carbonate deposits of the upper Badenian (Kosiv Formation – Wierbowiec Beds;  $N_1bd_3$ ; Andreyeva-Grigorovich *et al.*, 1997). Their thickness in the vicinity of the cave studied varies, depending on the relief, from 20 to 80 m. In their lower part (0–5 m), thin layers of sandstone and coquina limestone occur. The upper Badenian deposits form an erosional substrate for Quaternary alluvial gravel-sandy and loamy terrace deposits (3rd and 4th terraces of the Prut River valley; Andreychouk, 2007; Fig. 3).

#### MATERIAL

The Zoloushka Cave belongs to the largest gypsum caves of the Western Ukraine Gypsum Karst Region and is one of the largest gypsum caves in the world. The total length of its corridors is more than 90 km (Klimchouk, 1996; Klimchouk and Andreychouk, 2002; Andreychouk, 2007) and the area of its corridor network is up to several square kilometres (Fig. 4). The cave is developed within the top part of a 22–25-m-thick gypsum layer.

There are several types of palaeokarstic form present in the studied cave. Some of these forms are filled with material suitable for palynological studies, from which the first of the present authors collected samples during a speleological expedition in May, 2013. One sample was taken from carbonate draperies, another one from the clay-carbonate filling of contact pockets, and two samples were collected from laminated clays on the bottom of the cave corridors.

#### **Carbonate draperies**

The most common type of palaeokarst bodies in the Zoloushka Cave are carbonate draperies, protruding from the walls of the cave corridors and their ceilings (Fig. 5). These forms represent corrosively formed palaeofillings of karstified fissures in gypsum. Their filling consists of carbonate material (limestone), characterized by a different degree of cementation, consolidation and crystallization/ recrystallization. Carbonate bodies differ with regard to their high secondary porosity, the result of dissolution of their cement during the interaction with the waters which formed the cave. It is believed that the fissures are of lithogenetic (primary) origin and they were formed on the surface of the gypsum during the final stage of drying of the evaporitic basin (Andreychouk, 2007). They developed progressively on the surface of a freshly accumulated sulphate deposit, creating a distinct, polygonal network ("web of drying"). The gradual drying of the gypsum sediment was associated with further deepening of the fissures. In this way, they cut the gypsum to the depths from a few metres to 10 metres, or even more. Under the influence of atmospheric precipitation, the fissures underwent dissolution and their walls become uneven (karstified). During the period of non-accumulation (i.e. the interval between the final stage of gypsum formation and limestone deposition), the fissures underwent a further extension by corrosion, and they became traps for aeolian material, including, inter alia, pollen grains and spores.



![](_page_4_Picture_1.jpeg)

Fig. 5. Some examples of carbonate draperies protruding from the cave walls and ceilings: A. Drapery in Overture area. B. Drapery in Podvaly area.

![](_page_4_Figure_3.jpeg)

Fig. 6. A. Pocket filled with clastic clay-carbonate sediments at the contact of gypsum and limestone. B. Fissures in gypsum filled with the same material.

![](_page_4_Picture_5.jpeg)

Fig. 7. Thinly laminated cave clays covering the bottom of the cave corridors and galleries. A and B pictures show places where samples of clays were taken.

![](_page_5_Figure_2.jpeg)

![](_page_5_Figure_3.jpeg)

Fig. 8. Diagrams presenting proportions of sporomorphs of particular palaeofloristical elements in the samples studied. A. Carbonate draperies. B. Contact pockets. C. Laminated clays.

During the subsequent transgression, precipitation of carbonates from marine water took place, leading to the formation of a 0.5–1.2-m-thick chemogenic limestone layer. It covered the fissured and karstified gypsum surfaces, burying the carbonate and aeolian material (including palynological material) accumulated there during the preceding continental phase of karstification.

# Clay-carbonate fillings of pockets at the contact of gypsum and limestone

The ceiling of the cave passages in several places forms the corrosional "windows" in which a covering limestone layer (0.5-1.5 m) and a gypsum-limestone contact are clearly visible. In several places at the contact of gypsum and limestone, the presence of local palaeokarstic bodies (Fig. 6A), and fissures in gypsum (Fig. 6B) filled with clastic clay-carbonate material, were noted. The origin and age of these bodies have not yet been elucidated.

#### Laminated cave clays

The bottom of the cave galleries and corridors is covered by laminated cave clays. The thickness of these clays varies from 0.0 to 5.0-6.0 m, occasionally even more. The layer thickness ranges from 0.1 to 1.0-5.0 mm (Fig. 7). These clays represent strata deposited in an aquatic (phreatic) environment. The material was re-deposited in the aqueous cave environment and comes from the upper Badenian clays that cover the karstified gypsum-limestone series. The clay material entered the cave system through the collapse of the cave roofs. Breakdown cones were formed on the bottom of the corridors in the places where the roof had collapsed. Coarser material accumulated near the collapse locations, whereas loamy material was subsequently washed out (transported in suspension by underground water) and deposited in more distal cave areas, leading to the formation of laminated clays. These deposits may contain a mixture of palynological material, i.e., those from the marine upper Badenian clays, as well as those that occurred in the Quaternary loamy deposits that also fell into the cave during the collapse of the ceiling and the formation of sinkholes.

#### **METHODS**

The palynological samples from the Zoloushka Cave were processed in the Laboratory of the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, according to the modified Erdtman's acetolysis method (Moore et al., 1991). Additionally, hydrofluoric acid was used to remove mineral matter (silicates). The residuum was sieved at 5 µm on a nylon mesh. The microscope slides were made, using glycerine jelly or glycerine as a mounting medium and cover-slips  $24 \times 24$  mm. Depending on the frequency of sporomorphs (pollen grains and spores of plants), from 4-8 microscope slides from each sample were studied. In each sample, organic particles, sporomorphs and non-pollen palynomorphs (NPPs), such as dinoflagellate cysts, foraminifers and fungal remains were studied. Additionally, eight slides from the clastic clay-carbonate fillings of the karstified fissures were re-examined for dinoflagellate cysts. The rock samples, palynological residues and slides are stored in the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.

The sporomorph taxa identified were classified to an appropriate palaeofloristical element, mainly on the basis of the Atlas of Pollen and Spores of the Polish Neogene (Stuch-lik *et al.*, 2001, 2002, 2009, 2014). In the material studied, the following palaeofloristical elements were distinguished: palaeotropical (P), including: tropical (P1) and subtropical (P2), arctotertiary (A), including: warm-temperate (A1) and temperate (A2), and cosmopolitan (P/A). The proportions of the sporomorphs of the particular palaeofloristical elements are presented in Figure 8.

Microphotographs of selected sporomorphs and non-pollen palynomorphs (Figs 9, 10) were taken, using a NIKON Eclipse microscope, fitted with a Canon digital camera. Microphotographs of selected dinoflagellate cysts (Figs 11–19) were taken using a Carl Zeiss microscope and a Sony DSC-S75 camera.

# Table 1

Results of parynological analy	ysis (number of parynomorphs) of samples	from the z	Loiousn	ka Cav	e.		
TAXON	BOTANICAL AFFINITY	ELEMENT	carbonate draperies	contact pockets	laminated clays 1	laminated clays 2	
SPORES							
Baculatisporites sp.	Osmundaceae: Osmunda	P/A			2	1	
Distancoraesporis sp., Distverrusporis sp., Stereisporites spp.	Sphagnaceae: Sphagnum	P/A		81	6	1	
Laevigatosporites sp.	Polypodiaceae, Davalliaceae, and other ferns	P/A			14	3	
Leiotriletes sp.	?Lygodiaceae, ?Cyatheaceae	Р		1		1	
Neogenisporis sp.	p.p. Gleicheniaceae	P1		2			
<i>Radialisporis radiatus</i> (Krutzsch) Jansonius et Hills	Lygodiaceae, Parkeriaceae	P1		1			
Retitriletes sp.	Lycopodiaceae: Lycopodium	A	1	3	2	1	
Verrucatosporites sp.	Polypodiaceae, Dennstaedtiaceae	P/A			2		
	GYMNOSPERMS						
Abiespollenites sp.	Pinaceae: Abies	Α		2			
Cathayapollis spp.	Pinaceae: Cathaya	A1	2	2		1	
Cathayapollis sp., Pinuspollenites sp.	Pinaceae: Cathaya, Pinus haploxylon type	A	1	144	28	9	
Inaperturopollenites spp.	Cupressaceae: Taxodium, Glyptostrobus	P2/A1		60	2		
Keteleeriapollenites dubius (Khlonova) Słodkowska	Pinaceae: Keteleeria	A1		2		1	
Piceapollis spp.	Pinaceae: Picea	A	6	42	21	31	
Pinuspollenites labdacus (Potonié) Raatz	Pinaceae: Pinus sylvestris type	Α	165	289	62	152	
Sciadopityspollenites spp.	Sciadopityaceae: Sciadopitys	A1		22	1		
Sequoiapollenites sp.	Cupressaceae: Sequoia, Sequoiadendron, Metasequoia	A1		2	2		
Zonalapollenites spp.	Pinaceae: Tsuga	A	3	26	12	8	
bisaccates corroded	Pinaceae	A	22	224	30	15	
ANGIOSPERMS							
Aceripollenites sp.	Sapindaceae: Acer	A1				1	
Alnipollenites verus Potonié	Betulaceae: Alnus	P2/A	1	2	8	2	
Arecipites sp.	Amaryllidaceae, Araceae, Arecaceae, Butomaceae	P/A1		1			
Carpinipites carpinoides (Pflug) Nagy	Betulaceae: Carpinus	P2/A1		2	10	1	
Caryapollenites simplex (Potonié) Raatz	Juglandaceae: Carya	A1		7			
Celtipollenites sp.	Ulmaceae: Celtis	A1		1	1		
Chenopodipollis sp	Amaranthaceae (incl. Chenopodiaceae)	P/A			2	3	
Cichoreacidites gracilis (Nagy) Nagy	Asteraceae: Cichorioideae	А	1		3	10	
Cornaceaepollis satzveyensis (Pflug) Ziembińska-Tworzydło ex Jansonius et al.	Mastixiaceae	P1		1			
<i>Corylopsispollenites microreticulatus</i> E. Worobiec	Hamamelidaceae: Corylopsis	A1		1			
Cyperaceaepollis neogenicus Krutzsch	Cyperaceae	P/A			7	2	

Results of palynological analysis (number of palynomorphs) of samples from the Zoloushka Cave.

TAXON	BOTANICAL AFFINITY	ELEMENT	carbonate draperies	contact pockets	laminated clays 1	laminated clays 2
<i>Cyrillaceaepollenites exactus</i> (Potonié) Potonié	Clethraceae, Cyrillaceae	Р		1		
Edmundipollis sp.	Cornaceae, Mastixiaceae, Araliaceae	P/A1		1		
Ericipites spp.	Ericaceae	A	2	32	42	18
Faguspollenites sp.	Fagaceae: Fagus	A		6	22	6
Graminidites sp.	Poaceae: Pooideae	P/A			5	3
Intratriporopollenites insculptus Mai	Malvaceae: Brownlowioideae, Tilioideae	P/A1		2		
Juglanspollenites sp.	Juglandaceae: Juglans	A1		2	4	
Momipites sp.	Juglandaceae: Engelhardia, Alfaroa, Oreomunnea	P2		2		
Myricipites sp.	Myricaceae	P2/A1		1		
Nyssapollenites sp.	Nyssaceae: Nyssa	P2/A1		3		
Periporopollenites stigmosus (Potonié) Thomson et Pflug	Altingiaceae: Liquidambar	A1		2		
Persicarioipollis sp.	Polygonaceae: Polygonum	P/A				1
Plantaginacearumpollis miocaenicus Nagy	Plantaginaceae: Plantago	P/A			2	
Platycaryapollenites sp.	Juglandaceae: Platycarya	P2/A1		1		
Polyatriopollenites stellatus (Potonié) Pflug	Juglandaceae: Pterocarya	A1		2	1	1
<i>Quercoidites henrici</i> (Potonié) Potonié, Thomson et Thiergart ex Potonié	Fagaceae: Quercus	P2/A1		1		
Quercopollenites sp.	Fagaceae: Quercus	A1		1	3	
Salixipollenites sp.	Salicaceae: Salix	A			1	
Thalictrumpollis thalictroides Stuchlik	Ranunculaceae: Thalictrum	А			2	
<i>Tricolporopollenites pleurospermoides</i> E. Worobiec	Apiaceae	А				2
<i>Tricolporopollenites pseudocingulum</i> (Potonié) Thomson et Pflug	Styracaceae ? Fagaceae ?	P/A1		2		
Triporopollenites coryloides Pflug	Betulaceae: Corylus	A			4	1
Triporopollenites urticoides Nagy	Urticaceae: Urtica, Urera	P/A			5	
Trivestibulopollenites betuloides Pflug	Betulaceae: Betula	А		1		1
Tubulifloridites granulosus Nagy	Asteraceae: Asteroideae	P2/A			3	4
Ulmipollenites spp. + Zelkovaepollenites potoniei Nagy	Ulmaceae: Ulmus, Zelkova	A2, A1		14	8	
Vaclavipollis sp.	Caryophyllaceae	P/A			1	
corroded pollen grains	unknown	unknown		13	16	15
Sum of pollen and spores counted:			204	1005	334	295
SELECTED NON-POLLEN PALYNOMORPHS						
Dinoflagellate cysts (list of taxa given in Appendix 1)	Dinophyceae	X	2	223	3	3
Glomus sp.	Fungi: Glomeromycota	X			9	12
Arcella sp.	Amoebozoa: Arcella	Х			1	
Foraminifera	Foraminifera	X	15	63		

### **RESULTS OF PALYNOLOGICAL STUDIES**

In all of the studied samples, grey amorphous organic matter (AOM), presumably of marine and freshwater origins, occurs. No brown AOM particles, of terrestrial plant origin, are found.

All of the samples yielded various palynomorphs: pollen grains, spores of cryptogams (ferns, lycopods and mosses), dinoflagellate cysts and other non-pollen palynomorphs (Figs 9-19). In total, over 70 fossil species of sporomorphs (pollen and spores) and over 25 taxa of dinoflagellate cysts were identified. In most cases, in the text the taxa are listed in order, from the most common to rare ones, whereas a systematic listing of the spore and pollen fossil species and an alphabetic listing of dinoflagellate cysts are given in Appendices 1 and 2. The frequency of palynomorphs and the composition of their assemblages are different in particular samples (Tab. 1). Also palynomorph preservation varied - from excellently preserved specimens to completely corroded ones (especially bisaccate pollen grains) with a highly damaged structure. All the samples studied are very much dominated by bisaccate pollen grains, mainly Pinus. Strongly corroded, indeterminable specimens of bisaccate pollen are included to the "bisaccates corroded" group. Pollen grains of this group could represent Pinus, as well as Cathava, Cedrus, or others.

#### Sample from the carbonate draperies

The sample form the carbonate draperies yielded a small amount of organic particles and rare sporomorphs (Tab. 1). Eight pollen slides were examined, but only 203 pollen grains (including four pollen grains of angiosperms) were found. The most frequent are bisaccate pollen grains (mainly *Pinus sylvestris* type, and single specimens of *Picea* and *Cathaya*). Additionally, three specimens of *Tsuga* pollen were recorded. Angiosperms are represented only by single specimens of *Alnus*, Ericaceae and Asteraceae. Arctotertiary taxa are strongly dominant (Fig. 8), mainly because of a high frequency of *Pinus* pollen. Apart from pollen grains, one spore of *Lycopodium* as well as some remains of Foraminifera and two specimens of dinoflagellate cysts were encountered.

# Sample from the clastic clay-carbonate fillings of contact pockets

The palynofacies of this sample is dominated by terrestrial palynomorphs, mainly strongly destroyed bisaccate pollen grains. They are accompanied by well-preserved marine palynomorphs (dinoflagellate cysts and foraminifers) and usually small dispersed fragments of grey amorphous organic matter (AOM). Phytoclasts are represented mainly by unstructured, opaque, small, partly lath-shaped particles. Small fragments of charcoalified plant tissues are also present.

Each palynological slide from this sample contains about 1800–2000 pollen grains (including 150–200 pollen grains of angiosperms), 200 spores of plants, 120–150 dinoflagellate cysts, and some remains of Foraminifera. Although this sample is dominated by bisaccate pollen, more than 40 species of pollen and spores were recorded. The pollen spectrum from this sample is rich in taxa, but many of them occur as single specimens (Tab. 1). Among the bisaccates Pinus sylvestris type, Pinus haploxvlon type/ Cathaya and Picea are dominant, while Abies and Keteleeria occur subordinately. The non-bisaccate pollen grains of conifers are represented by Taxodium/Glyptostrobus, Tsuga, Sciadopitys, and single specimens of Sequoia. Among deciduous trees and shrubs, the pollen of Ulmus/Zelkova, Carya, Fagus, and Nyssa is the most frequent. Additionally, pollen grains of Carpinus, Engelhardia, Juglans, Pterocarya, and single specimens of many others, are present. Among shrubs, the pollen of Ericaceae predominates. Cryptogams are represented mainly by the spores of Sphagnum, single ferns and lycopods.

Arctotertiary palaeofloristical elements are dominant (Fig. 8), which is also caused mainly by the high frequency of *Pinus* pollen. Nevertheless, pollen and spores representing palaeotropical elements are taxonomically variable (Tab. 1). The palaeotropical elements are represented mainly by subtropical and palaeotropical/warm-temperate taxa (e.g., spores of *Leiotriletes* sp., *Neogenisporis* sp., and *Radialisporis radiatus*, as well as pollen grains of *Arecipites* sp. (palm?), *Cornaceaepollis satzveyensis*, *Cyrillaceaepollenites exactus*, *Edmundipollis* sp., *Inaperturopollenites* sp., *Intratriporopollenites insculptus*, *Momipites* sp., *Myricipites* sp., *Nyssapollenites* sp., *Platycaryapollenites* sp., *Quercoidites henrici*, and *Tricolporopollenites pseudocingulum*).

Dinoflagellate cysts are fairly well-preserved and pale-coloured (Figs 11–19). Some larger specimens show a darker colouration, which reflects rather the wall thickness (e.g., *Spiniferites pseudofurcatus, Systematophora* sp. or large species of *Operculodinium*). The dinoflagellate cyst assemblage (Appendix 1) consists of over 25 taxa (genera *Spiniferites* and *Achomosphaera* were determined mainly to the generic level). Despite this, it shows a low diversity being dominated by the genus *Spiniferites* (and morphologically similar *Achomosphaera*) – over 70%. *Operculodinium centrocarpum* represents 10%, *Systematophora* sp. – 4%. Other species are rare, or they are present as single specimens only.

#### Samples from the laminated cave clays

The palynofacies of these samples is characterised by the predominance of amorphous organic matter (AOM) and phytoclasts (both structured and amorphous). The proportion of AOM to phytoclasts is variable, as is the size of the phytoclast particles. Phytoclasts are represented by usually lath-shaped, translucent wood and cuticle remains, opaque structured charcoal and structureless particles with usually sharp edges. These particles are usually small to very small. Palynomorphs are represented by relatively infrequent pollen grains, usually corroded. In both samples studied, spores of arbuscular mycorrhizal fungi *Glomus* were recorded. In addition, some remains of testate amoeba *Arcella* were found. Marine palynomorphs are represented by single specimens of dinoflagellate cysts.

![](_page_9_Figure_1.jpeg)

**Fig. 9.** Pollen grains and spores from the contact pockets. Botanical affinity in brackets. All scale bars – 20 μm. **A.** Zonalapollenites verrucatus (Tsuga). **B.** Cathayapollis cf. potoniei (Cathaya). **C.** Sciadopityspollenites serratus (Sciadopitys). **D.** Inaperturopollenites concedipites (Taxodium/Glyptostrobus). **E.** Sequoiapollenites sp. (Sequoia). **F.** Momipites sp. (Engelhardia). **G.** Alnipollenites verus (Alnus). **H.** Ericipites baculatus (Ericaceae). **I.** Retitriletes sp. (Lycopodium). **J.** Stereisporites cyclus (Sphagnum). **K.** Stereisporites stereoides (Sphagnum).

In both samples from the laminated cave clays, about 100-300 pollen grains and a few plant spores per slide were encountered. Bisaccate pollen related to conifers (Pinaceae) predominates among the pollen grains. Among conifers, the pollen grains of Pinus (mainly Pinus sylvestris type) are the most frequent. The pollen of Picea, Tsuga, and Cathaya are also common. Conifers other than Pinaceae are represented by single specimens of Taxodium/ Glyptostrobus, Sequoia, and Sciadopitys. Deciduous trees are represented mainly by Fagus, Carpinus, Alnus, Ulmus/ Zelkova, Corylus, Juglans, Pterocarya, Quercus, and some others. Among shrubs, the pollen of Ericaceae (mainly the fossil species Ericipites baculatus) predominates. Herbs are common, and among them Asteraceae, Cyperaceae, Poaceae, Urticaceae, Chenopodiaceae, Apiaceae, Plantago, and Thalictrum occur. Spores are represented mainly by Polypodiaceae s.l. (ferns), Osmunda, Sphagnum, and Lycopodium (Tab. 1).

The composition of sporomorph associations from the laminated cave clays shows an apparent predominance of arctotertiary (including warm-temperate and temperate) and cosmopolitan palaeofloristical elements (Tab. 1, Fig. 8).

#### INTERPRETATION BASED ON THE RESULTS OF THE PALYNOLOGICAL STUDIES

The pollen spectra studied are dominated by bisaccate pollen (mainly Pinus svlvestris type and similar corroded bissaccates), which is always over-represented, especially in marine sediments, owing to the high pollen productivity of Pinus trees, and because its morphology is favourable for long-distance atmospheric and hydrologic (buoyancy) transportation. Additionally, Pinus and Picea are two of the most corrosion-resistant pollen taxa, because of a high sporopollenin content in the walls of their pollen grains (Tomescu, 2000). Pollen assemblages with a high proportion of degraded grains and with over-representation of resistant grains are characteristic for many cave deposits (Groner, 2004). Therefore, the pollen spectra recorded may be used for the reconstruction of past environments and palynostratigraphic correlations only with great caution. Nevertheless, the palynological assemblages provide important information, supplementing knowledge of the palaeoenvironment and palaeoecology of the site as well as the sedimentation of the deposits studied.

#### Palynoflora from the carbonate draperies

The pollen assemblage from the carbonate draperies has limited value for age determination and palaeoenvironmnet reconstruction. The occurrence of some "pre-Quaternary elements", such as *Cathaya* and *Tsuga*, points to the Neogene age of at least some pollen grains. Additionally, the presence of similar pollen grains and non-pollen palynomorphs in this sample and in the other samples from the Zoloushka Cave indicates a similar age for at least some of the palynomorphs recorded in all of the samples from the Zoloushka Cave. The presence of foraminifera in the deposits from the carbonate draperies indicates a marine sedimentary environment.

#### Palynoflora from the clastic clay-carbonate fillings of contact pockets

The presence of numerous dinoflagellate cysts and the lack of freshwater algae in the sample from the clastic clay-carbonate fillings of contact pockets show that they were deposited in a marine environment. The composition of the assemblage indicates an offshore setting, beyond the zone of accumulation of terrestrial organic matter (pollen grains present in the sample studied could have been transported by wind). Nematosphaeropsis and Impagidinium, both present in the material studied, are regarded as offshore species that inhabit oceanic waters (e.g., Brinkhuis, 1994). Their occurrence in the sample studied resembles the described late Badenian assemblages of Kudryntsi (Western Ukraine), particularly from the M sample, which contains very frequent Spiniferites with subordinate Impagidinium and Nematosphaeropsis. The palaeoenvironmental interpretation of dinoflagellate cysts and foraminifera (domination of miliolids) from that Kudryntsi sample, collected above the Ratyn Limestone, indicates that it was deposited in a relatively shallow, but offshore basin with slightly increased salinity (Gedl and Peryt, 2011).

The results of classical spore-pollen analysis of the sample show an important role of mixed forests composed of Ulmus, Carya, Fagus, Carpinus, Juglans, Pterocarya, Quercus, Tilioideae, Liquidambar, Juglans, Zelkova, and conifers, with an admixture of thermophilous taxa, such as Engelhardia, Platycarya, and ferns (e.g., Gleicheniaceae) in the neighbouring area. Some pollen grains of Pinaceae (Pinus, Picea, Abies and Tsuga) possibly come from plant communities growing on elevated terrains, at a distance (maybe also a great distance) from the locality. Nevertheless, conifers were most probably important trees in the mixed forests, or some of them (for example Pinus) formed their own plant communities in the vicinity. Ericaceae were presumably a component of the groundcover of the forests, or they formed open dwarf-shrub communities, such as bush swamps. Sphagnum (commonly called peat moss) and Ericaceae probably also contributed to the formation of peat bogs. Taxodium, Nyssa, and presumably Glyptostrobus were components of swamp forests that might have overgrown the neighbouring area with a higher groundwater level.

#### Age interpretation of the clastic clay-carbonate fillings of contact pockets based on the dinoflagellate cysts assemblage

Most of dinoflagellate cyst species from the clastic clay-carbonate fillings studied have long stratigraphic ranges, which do not allow the precise dating of the material studied. *Labyrinthodinium truncatum* is a species with a relatively narrow stratigraphic range, limited to Langhian and Tortonian (e.g., Stover *et al.*, 1996). De Verteuil and Norris (1996) reported the lowest occurrence of this species in the mid-latitudes in the lowermost Langhian (correlated

with the upper part of NN4 Zone and the basal part of the N8 Zone) and its highest occurrence in the upper Tortonian (correlated with the middle part of the calcareous nannoplankton NN11 Zone and the middle part of the planktonic foraminifera N17 Zone). Zevenboom (1995) reported *L. truncatum* in the Mediterranean as occurring from the middle Langhian to the middle Tortonian.

More precise dating of the sample studied can be indicated by the absence of the typical Serravallian species Unipontidinium aquaeductum. The occurrence of this species is usually restricted to the topmost Langhian and mid Serravalian (e.g., Manum, 1976; Piasecki, 1980; Edwards, 1984; Powell, 1986; Head et al., 1989; Manum et al., 1989; Powell, 1992; Zevenboom, 1995). Its absence indicates that the age of the sample studied can be either Langhian or late Serravalian-Tortonian. The comparison of the Zoloushka dinoflagellate cyst assemblage with the ones from the Polish and Ukrainian Carpathian Foredeep does not give an unequivocal solution of the age of the sample. The U. aquaeductum described was found in the basinal facies of the pre-evaporite deposits (the so-called Skawina Beds, or their equivalents; e.g., Gedl, 1996, 1997, 2005; Peryt and Gedl, 2010) correlated with the NN5-lowermost NN6 zones (Garecka et al., 1996; Peryt, 1997), i.e., with the upper part of Langhian and the lower part of Serravalian (Berggren et al., 1995). It is not correlated with the post-evaporite deposits (Gedl, 1999; Gedl and Peryt, 2011) correlated with the NN6-NN7 zones (Peryt, 1997; see also Oszczypko, 1999). Palaeocystodinium striatogranulatum is another characteristic species that is not present in the sample studied. Zevenboom (1995) reported a relatively wide stratigraphic range for this species (Burdigalian-early Tortonian) but its occurrence in the Carpathian Foredeep succession is limited to the pre-evaporite part only (Gedl, 1999, 2005) that is not younger than the NN5 Zone, i.e., Langhian-lower Serravalian.

The general taxonomical composition of the assemblage from the studied sample shows similarities to the ones described basing on the post-evaporate deposits. This refers to the assemblages from the Jamnica S-119 borehole (southern Poland), particularly to the one from the middle and upper parts of the *Pecten* Beds (Interval II *sensu* Gedl, 1999), which consist of frequent specimens of *Nematosphaeropsis* and *Spiniferites*, associated with most of the species also known from the Zoloushka Cave. Taxonomically similar assemblages were described by Gedl and Peryt (2011), on the basis of the deposits above the Ratyn Limestone (the Kosiv Suite) at Kudryntsi (western Ukraine); they also contain most of the Zoloushka species, with frequent *Spiniferites*.

These circumstances show that the sample from the clastic clay-carbonate fillings of the contact pockets from the Zoloushka Cave represents most likely post-evaporite deposits that were accumulated during the late Badenian (i.e., late Serravalian, correlated with the upper part of the NN6 Zone and/or NN7 Zone).

#### Palynoflora from the laminated clays

This assemblage probably contains mixed pollen grains and spores, both Neogene and Quaternary in age.

The characteristics of the sedimentary organic matter point to a probable freshwater origin of the deposit. The rather small size of phytoclasts and the destruction of most palynomorphs could indicate re-deposition of them in a fluvial environment of at least moderate energy, or their soil origin. The presence of the spores of arbuscular mycorrhizal fungi (AMF) – microorganisms which occur below the ground (in soil), also indicates this.

Classical spore-pollen analysis of the laminated clays revealed the presence of some "pre-Quaternary elements", such as *Pterocarya*, *Tsuga*, *Sequoia*, and *Ca-thaya*. Nevertheless, most of the sporomorphs have long stratigraphic ranges. Owing to the re-deposition and mixing of the Neogene and Quaternary sporomorphs in the laminated clays, reconstruction of plant communities is impossible.

# Comparison of the spore-pollen assemblages studied with the Badenian palynofloras from Ukraine

The pollen assemblages from the Zoloushka Cave contain many "Neogene elements" and show similarities to the middle Miocene (especially Badenian) spore-pollen assemblages described at many European localities (e.g., Mai, 1981, 1995; Piwocki and Ziembińska-Tworzydło, 1997; Ważyńska, 1998; Ivanov *et al.*, 2011). They are especially similar to the Badenian palynofloras in Ukraine (e.g., Syabryaj *et al.*, 2007). These similarities are especially visible in the pollen assemblage from the fillings of the contact pockets.

The middle Miocene vegetation in the Ukrainian Carpathians was dominated by broadleaved forests with Ulmus, Castanea, frequent Engelhardia, and many other plants (Iljinskaya, 1960; Syabryaj et al., 2007). On the outer slopes of the Ukrainian Carpathian Mountains, forests with Picea and Ulmus became more important. In this area, thermophilous species disappeared, which points to cooler climatic conditions by comparison with the inner zone of the Ukrainian Carpathians (Syabryaj et al., 2007; Ivanov et al., 2011). During the late Badenian in the Ukrainian Carpathians, humid coastal and riparian forests with Carva, Pterocarva, Liquidambar, Alangium, and Myrica played an important role. The mixed forests included Juglans, Engelhardia, Tilioideae, Acer, Castanea, Fagus, and Quercus, as well as Platycarya, Zelkova and Ulmus. The shrub layer became more diverse (Syabryaj and Stuchlik, 1994; Syabryaj et al., 2007; Ivanov et al., 2011).

The following amplitudinal vegetation zones were reconstructed for the mountain regions during the late Badenian: in the foothills area, marginal assemblages of moisture-loving plants as thermophilous ferns and marshes, including swamp forests with *Taxodium* and marshy shrub vegetation in the marginal part of the swamps; in the lower mountain zone, warm-temperate deciduous forests (with *Juglans, Liquidambar, Engelhardia, Castanea, Platycarya*, and others) with a considerable amount of subtropical elements, including such shrubs as Lauraceae (identified as *Cinnamomum*) and Myrtaceae; in the upper mountain zone warm-temperate deciduous, deciduousconiferous, and coniferous forests including *Abies, Picea*,

![](_page_12_Figure_1.jpeg)

Fig. 10. Pollen grains and one non-pollen palynomorph from the laminated clays. Botanical affinity in brackets. All scale bars – 20 μm. A. *Piceapollis tobolicus (Picea)*. B. *Sequoiapollenites* sp. (*Sequoia)*. C. *Alnipollenites verus (Alnus)*. D. *Zonalapollenites robustus (Tsuga)*. E. *Ulmipollenites maculosus (Ulmus)*. F, G. *Thalictrumpollis thalictroides (Thalictrum)*; same specimen, various foci. H, I. *Ericipites callidus* (Ericaceae); same specimen, various foci. J. *Ericipites baculatus* (Ericaceae). K. *Glomus* sp. (spore of arbuscular mycorrhizal fungus).

![](_page_13_Figure_1.jpeg)

**Fig. 11.** Dinoflagellate cysts from the contact pockets. All scale bars – 25 μm. **A, B.** *Spiniferites ramosus*. **C.** *Spiniferites pseudofurcastus*. **D.** *Spiniferites ramosus*. **E, F.** *Spiniferites* sp. with membranous septa joining processes in antapical area, resembling *Spiniferites mirabilis*; same specimen, various foci. **G–J.** *Spiniferites* sp.: species with very low and thin parasutural ridges and relatively thick endophragm; same specimen, various foci. **K, L.** *Spiniferites* sp.: species with long and faint processes; same specimen, various foci. **M, N.** *Spiniferites ramosus*. **O, P.** *Achomosphaera* sp.: species with intergonal processes; same specimen, various foci. **Q, R.** *Spiniferites ramosus*; same specimen, various foci.

*Tsuga*, *Cedrus*; and above the timberline alpine meadows (Syabryaj and Stuchlik, 2004). The valleys were overgrown by riparian forests with abundance of *Alnus* (Shvarieva, 1983; Syabryaj and Stuchlik, 2004). Towards the end of the Badenian, subtropical assemblages and communities with thermophilous ferns slightly diminished. The increasing amount of herbaceous pollen, chiefly of plants from the mountain meadow communities, indicates the appearance of open areas on a high altitude of the rising mountains (Syabryaj and Stuchlik, 1994, 2004; Syabryaj *et al.*, 2007; Ivanov *et al.*, 2011).

The middle Miocene vegetation in the plain areas of Ukraine was represented by polydominant broadleaved forests with *Quercus*, *Ulmus*, *Zelkova*, *Castanea*, *Liquidambar*, *Fagus*, *Pterocarya*, *Juglans*, and *Carpinus*. The undergrowth of these forests consisted of *Corylus*, *Erica*, Lauraceae, *Buxus*, *Ilex*, Arecaceae, and Theaceae. In river valleys and around lakes, riparian forest, dominated by *Salix* and *Alnus*, grew. Swamp forests with *Taxodium* occurred in the Crimea Peninsula as well as in the humid, continental area. The presence of *Keteleeria*, *Tsuga*, *Cedrus*, *Picea*, and Cupressaceae indicates the expansion of coniferous forests. Additionally, some herb species were also present (Syabryaj et al., 2007; Ivanov et al., 2011).

In the middle Badenian (at the end of the Karaganian) a wide river system spread across the Ukraine Plain. Large watershed areas were occupied by pine forests, whereas forests with *Taxodium* were less important. Mesophyllous, polydominant forests with *Quercus*, *Ulmus*, *Fagus*, *Zelkova*, *Alnus*, *Celtis* as well as *Carpinus*, *Acer*, *Carya*, *Castanea*, *Fraxinus*, *Rhus*, *Nyssa*, and *Liquidambar*, occupied territories with richer soils. The late Karaganian regression indicated more arid conditions, and the climate became more continental. As a result of the regression, larger areas of the continental shelf became land, which was quickly occupied by terrestrial herbs, such as halophilous members of the Chenopodiaceae (Syabryaj et al., 2007).

During the late Badenian, in the territory of contemporary Northern Prichernomor'e and further to the north, coniferous forests with different species of *Pinus* predominated. Broadleaved forests were diverse, but some impoverishment of these communities has been observed. Swamp forests with *Taxodium* nearly disappeared. The expansion of herbaceous communities, with members of the Chenopodiaceae family, took place (Syabryaj *et al.*, 2007).

# PALAEOKARSTIC INTERPRETATION

The results of the studies by the authors also allow some conclusions on the palaeokarst formation and its origin to be suggested.

In the case of the laminated cave clays, the authors generally confirm their origin as re-deposited clayey sediments, originating from the upper Badenian and Quaternary series that overlie the cave. The composition of the sedimentary organic matter and pollen assemblage in the samples indicates it. The presence of the spores of arbuscular mycorrhizal fungi (*Glomus* sp.) in the studied samples points to the transport (gravitational – due to the collapse) of soil material into the cave. Additionally, the spores may have been produced by mycorrhizal mycelia related to AMF host plants, the roots of which grew into the layer where the deposits lie (Kołaczek *et al.*, 2013).

In the case of the carbonate draperies, the situation is not so clear because of a relatively poor nature of the pollen assemblage. Nevertheless, the occurrence in the sample studied of such "pre-Quaternary elements" as Cathava and Tsuga, generally points to a Neogene age for the draperies material. It corresponds with the hypothesis that the draperies represent the palaeofillings of primary fissures formed on the surface of the gypsum after the drying up of the upper Badenian evaporite basin. Some remains of Foraminifera and two specimens of dinoflagellate cysts in the sample from the draperies show that they were formed in marine conditions. Most likely, this was the result of the transgression, which finalized the upper Badenian evaporitic cycle and after which also the layer of chemogenic limestone remained covering the karstified surface of gypsum.

In the case of the clastic clay-carbonate fillings of the contact pockets, as opposed to the previous ones, the situation is clearer, both in terms of their age and the genetic environment. The composition of their spore-pollen assemblage, sedimentary organic matter, and the lack of freshwater algae all point to a fully marine sedimentary setting. Comparing them with the assemblages described at other places in the Western Ukraine, the authors assume their age to be late Badenian (change phase). This convincingly shows that a short break in sedimentation took place after formation of the gypsum layer (before the formation of limestone overlying the gypsum), which resulted in the karstification of lithogenetic fissures at the gypsum surface and the surface in general (small depressions on the surface - the future sites of the pockets). The clastic nature of the fillings of the pockets may indicate the circumstances of accumulation of the material, as a result of the washing out of it from the weathered and karstified gypsum surface by heavy rain.

#### CONCLUSIONS

The palynological study confirms an earlier hypothesis (Andreychouk, 2007) about the presence of a sedimentation break of short duration between the formation of the gypsum and the limestone overlying it at the end of the upper Badenian evaporitic cycle in the Western Ukraine region. Numerous palaeokarst formations present in the Zoloushka Cave (Bukovina area), such as carbonate draperies and clay-carbonate fillings of corrosional pockets and fissures at the contact of gypsum and overlying limestone, indicate the break. Pollen and dinoflagellate cysts generally confirm the late Badenian age of the formations and point to their origin as palaeokarstic forms that arose on the gypsum surface during the sedimentation break. Owing to the marine transgression, karst forms developed in the gypsum and their surface was filled with carbonate material (draperies) or clay-carbonate clastic material (pockets and fissures) chemogenically deposited from sea water.

![](_page_15_Figure_1.jpeg)

**Fig. 12.** Dinoflagellate cysts from the contact pockets. All scale bars – 25 μm. **A–C.** *Achomosphaera* sp.: species with moderately thick and coarsely ornamented endophragm and thin gonal processes (*A. crassipellis?*); B, C – same specimen, various foci. **D, E.** *Achomosphaera* sp.: species with thin and smooth endophragm and gonal processes; same specimen, various foci. **F, H, J.** *Achomosphaera* sp.: species with intergonal processes; same specimen, various foci. **G, I.** *Spiniferites pseudofurcatus*; same specimen, various foci.

![](_page_16_Figure_1.jpeg)

**Fig. 13.** Dinoflagellate cysts from the contact pockets. All scale bars – 25 μm. **A–I.** *Spiniferites ramosus*; A and B, C and D, E and F, G and H – same specimens, various foci. **J–L.** *Spiniferites* sp.: species with short gonal processes terminated with small trifurcations. **M.** *Spiniferites ramosus*. **N–T.** *Impagidinium aculeatum*; N–P, Q and R, S and T – same specimens, various foci.

![](_page_17_Figure_1.jpeg)

**Fig. 14.** Dinoflagellate cysts from the contact pockets. All scale bars – 25 μm. **A, B.** *Impagidinium*? sp. **C, D.** *Impagidinium aculeatum*; same specimen, various foci. **E.** *Impagidinium*? sp. **F–H.** *Nematosphaeropsis labyrinthus*; same specimen, various foci. **I–K.** *Nematosphaeropsis lemniscata*; same specimen, various foci. **L–N.** *Nematosphaeropsis labyrinthus*; same specimen, various foci. **O, S, W.** *Nematosphaeropsis lemniscata*; same specimen, various foci. **P–R.** *Nematosphaeropsis labyrinthus*; same specimen, various foci. **T–V.** *Nematosphaeropsis labyrinthus*; same specimen, various foci. **T–V.** *Nematosphaeropsis labyrinthus*; same specimen, various foci. **T–V.** *Nematosphaeropsis labyrinthus*; same specimen, various foci.

![](_page_18_Figure_1.jpeg)

**Fig. 15.** Dinoflagellate cysts from the contact pockets. All scale bars  $-25 \ \mu m$ . **A–D.** *Operculodinium* sp.: small species with smooth wall and short, proximally wide, distally narrowing capitate processes; A and B, C and D – same specimens, various foci. **E–L.** *Operculodinium centrocarpum*; F and G, H and I, J–L – same specimens, various foci. **M, N.** *Operculodinium* sp.: small species with regulate moderately thick wall and short, blade-like processes; same specimen, various foci. **O** *Operculodinium centrocarpum*. **P, Q, S–U.** *Operculodinium* sp.: large species with finely granulate wall and very short, tubular processes distally slightly expanded; P and Q, S–U – same specimens, various foci. **R.** *Operculodinium* sp.: species with smooth cyst wall and relatively long solid processes.

![](_page_19_Figure_1.jpeg)

**Fig. 16.** Dinoflagellate cysts from the contact pockets. All scale bars –  $25 \mu m$ . **A–C.** *Lingulodinium machaerophorum*; same, incomplete specimen, various foci. **D–P.** *Systematophora* sp.: specimens representing this genus show various structure of the cyst wall from moderately (D and G) through coarsely granular (N–P); proximal circular ridges joining bases of the processes show various stages of development: some specimens bear incomplete ones (D and G, E and F) being similar to S. *ancyrea*; the ones with more complete ridges (K–M) represent presumably *S. placacantha*.

![](_page_20_Figure_1.jpeg)

**Fig. 17.** Dinoflagellate cysts from the contact pockets. All scale bars – 25 μm. **A–C.** *Melitasphaeridium choanophorum*; same specimen, various foci. **D, E.** *Dapsilidinium pseudocolligerum*; same specimen, various foci. **F–H.** *Reticulatosphaera actinocoronata*; same specimen, various foci. **I–K.** *Melitasphaeridium pseudorecurvatum*; same specimen, various foci. **L–N.** *Reticulatosphaera actinocoronata*; same specimen, various foci. **O, P, T.** *Reticulatosphaera actinocoronata*; same specimen, various foci; most of specimens of *R. actinocoronata* in the material studied have isolated processes. **Q–S.** *Dapsilidinium pseudocolligerum*; same specimen, various foci; most foci. **U–W.** *Homotryblium* sp.: poorly preserved specimen with smooth wall and processes terminated distally with short spines, may represent *H. pallidum* or *H. aculeatum*; presumably reworked; same specimen, various foci. **X.** *Dapsilidinium pseudocolligerum*. **Y, Z.** *Polysphaeridium subtile*; same specimen, various foci.

![](_page_21_Picture_1.jpeg)

**Fig. 18.** Dinoflagellate cysts from the contact pockets. All scale bars – 25 µm. **A–F.** *Hystrichokolpoma* cf. *salacia*; A–C, D–F – same specimens, various foci. **G–J.** *Pentadinium laticinctum*; H–J – same specimen, various foci.

![](_page_22_Figure_1.jpeg)

**Fig. 19.** Dinoflagellate cysts and acritarchs from the contact pockets. All scale bars – 25 μm. **A, B.** *Svenkodinium* sp.; same specimen, various foci. **C–L.** *Batiacasphaera*? sp.; C–E, F–H, I and J, K and L – same specimens, various foci. **M–R.** *Batiacasphaera sphaerica*; M–O, P–R – same specimens, various foci. **S, T.** *Batiacasphaera* sp. **U, V.** *Batiacasphaera sphaerica*; same specimen, various foci. **W–Z.** *Pyxidinopsis* sp.; W, X – same specimen, various foci. **Z1–Z4.** *Labyrinthodinium truncatum*; Z1 and Z2, Z3 and Z4 – same specimens, various foci.

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Appendix 1. An alphabetic listing of dinoflagellate cysts from sample from the contact pockets

Achomosphaera spongiosa Matsuoka et Bujak 1988	Homotryblium sp.
Achomosphaera sp.	Hystrichokolpoma rigaudiae Deflandre et Cookson 1955
Batiacasphaera sphaerica Stover 1977	Hystrichokolpoma cf. salacia Eaton 1976
Batiacasphaera? sp.	Impagidinium aculeatum (Wall 1967) Lentin et Williams 1981
Dapsilidinium pseudocolligerum (Stover 1977) Bujak et al. 1980	Impagidinium? sp.

Labyrinthodinium truncatum Piasecki 1980	Pentadinium sp.
Lingulodinium machaerophorum (Deflandre et Cookson 1955) Wall 1967	Polysphaeridium subtile Davey et Williams 1966
Melitasphaeridium choanophorum (Deflandre et Cookson 1955)	Polysphaeridium zoharyi (Rossignol 1962) Bujak et al. 1980
Harland et Hill 1979	Pyxidinopsis sp.
Melitasphaeridium pseudorecurvatum (Morgenroth 1966) Bujak	Reticulatosphaera actinocoronata (Benedek 1972) Bujak et Mat-
<i>et al.</i> 1980	suoka 1986
Nematosphaeropsis labyrinthus (Ostenfeld 1903) Reid 1974	Spiniferites pseudofurcatus (Klumpp 1953) Sarjeant 1970
Nematosphaeropsis lemniscata Bujak 1984	Spiniferites ramosus (Ehrenberg 1838) Mantell 1854
Operculodinium centrocarpum (Deflandre et Cookson 1955) Wall 1967	Spiniferites spp.
Operculodinium spp.	Systematophora sp.

Appendix 2. Systematic listing of spore and pollen fossil species as well as other microfossils from the material studied

BRYOPHYTINA (mosses)

Distancoraesporis sp.

Distverrusporis sp.

Stereisporites cyclus Krutzsch 1963

Stereisporites stereoides (Potonié et Venitz 1934) Thomson et Pflug 1953 Stereisporites sp.

LYCOPHYTINA (lycopods) *Retitriletes* sp.

PTEROPHYTINA (ferns) Baculatisporites sp. Laevigatosporites sp. Leiotriletes sp. Neogenisporis sp. Radialisporis radiatus (Krutzsch 1959) Jansonius et Hills 1976 Verrucatosporites sp.

#### PINOPHYTINA (gymnosperms)

Abiespollenites sp. Cathayapollis cf. potoniei (Sivak 1976) Ziembińska-Tworzydło 2002 Cathayapollis pulaënsis (Nagy 1985) Ziembińska-Tworzydło 2002 Cathavapollis sp. Inaperturopollenites concedipites (Wodehouse 1933) Krutzsch 1971 Inaperturopollenites sp. Keteleeriapollenites dubius (Khlonova 1960) Słodkowska in Ziembińska-Tworzydło et al. 1994 Piceapollis tobolicus (Panova 1966) Krutzsch 1971 Piceapollis sp. Pinuspollenites labdacus (Potonié 1931) Raatz 1937 ex Potonié 1958 Pinuspollenites sp. Sciadopityspollenites serratus (Potonié et Venitz 1934) Raatz 1937 ex Potonié 1958 Sciadopityspollenites sp. Sequoiapollenites sp. Zonalapollenites robustus Krutzsch 1971 ex Kohlman-Adamska 1993 Zonalapollenites verrucatus Krutzsch 1971 ex Ziembińska-Tworzydło 1974 Zonalapollenites sp. MAGNOLIOPHYTINA (angiosperms)

Aceripollenites sp. Alnipollenites verus Potonié 1931 Arecipites sp. Carpinipites carpinoides (Pflug in Tomson et Pflug 1953) Nagy 1985 Caryapollenites simplex (Potonié 1939) Raatz 1937 ex Potonié 1960 Celtipollenites sp. Chenopodipollis sp Cichoreacidites gracilis (Nagy 1969) Nagy 1985 Cornaceaepollis satzveyensis (Pflug in Tomson et Pflug 1953) Ziembińska-Tworzydło in Ziembińska-Tworzydło et al. 1994 ex Jansonius et al. 1998 Corylopsispollenites microreticulatus E. Worobiec 2014 Cyperaceaepollis neogenicus Krutzsch 1970 Cyrillaceaepollenites exactus (Potonié 1931) Potonié 1960 Edmundipollis sp. Ericipites baculatus Nagy 1969 Ericipites callidus (Potonié 1931) Krutzsch 1970 Ericipites sp. Faguspollenites sp. Graminidites sp. Intratriporopollenites insculptus Mai 1961 Juglanspollenites sp. Momipites sp. Myricipites sp. Nyssapollenites sp. Periporopollenites stigmosus (Potonié 1931) Thomson et Pflug 1953 Persicarioipollis sp. Plantaginacearumpollis miocaenicus Nagy 1963 Platycaryapollenites sp. Polyatriopollenites stellatus (Potonié 1931) Pflug 1953 Quercoidites henrici (Potonié 1931) Potonié, Thomson et Thiergart 1950 ex Potonié 1960 Quercopollenites sp. Salixipollenites sp. Thalictrumpollis thalictroides Stuchlik 2009 Tricolporopollenites pleurospermoides E. Worobiec 2014 Tricolporopollenites pseudocingulum (Potonié 1931) Thomson et Pflug 1953 Triporopollenites coryloides Pflug in Thomson et Pflug 1953 Triporopollenites urticoides Nagy 1969 Trivestibulopollenites betuloides Pflug in Thomson et Pflug 1953 Tubulifloridites granulosus Nagy 1969 Ulmipollenites maculosus Nagy 1969 Ulmipollenites sp. Vaclavipollis sp. Zelkovaepollenites potoniei Nagy 1969

#### OTHER MICROFOSSILS

*Arcella* sp. *Glomus* sp.